RELATIONSHIP OF RUMEN FLUID DILUTION RATE TO RUMEN FERMENTATION AND DIETARY CHARACTERISTICS OF BEEF STEERS[1,2]

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Summary

Data from seven beef steer trials were compiled and regression analyses used to evaluate relationships among molar proportions of acetate (Ac), propionate (Pr) and butyrate (Bu), total concentration of volatile fatty acids (VFA), rumen ammonia (NH_3), rumen pH, rumen fluid dilution rate (FDR), rumen fluid volume (FVOL), body weight (WT), dry matter intake (DMI) and dietary concentration and intake of crude protein (CP and CPI), acid detergent fiber (ADF and ADFI), ash (ASH and ASHI) and metabolizable energy (ME and MEI). Of the six fermentation variables, Pr (negative regression coefficient, β) and pH (positive β) were related ($P<.05$) to FDR, but only 3 and 12% of the variation in these two variables, respectively, was explained by FDR. When FDR was described by dietary characteristics, ASHI was positively related to FDR (R^2 = .16). The best two-variable model for FDR contained DMI (positive β) and WT (negative β) and increased R^2 to .36. Fluid volume was best described by ME (positive β; R^2 = .20). The two-variable model for FVOL added ASH with a positive partial β (R^2 = .23). When fermentation variables were regressed on dietary characteristics, Ac was best described by ADF (positive β; R^2 = .71). The variable that best described Pr proportion was ADF (negative β; R^2 = .50), and addition of CP (negative β) and MEI (positive β) into the Pr model improved R^2 to .70. Molar proportion of butyrate was related to CP (positive β; R^2 = .23), and addition of ME (positive β) to the model improved the R^2 to .31. Total VFA concentration was best described by ADFI (positive β; R^2 = .14). An R^2 of .29 resulted when ME (positive β) and CPI (negative β) were included in the total VFA model. Rumen pH was related to ADF (positive β; R^2 = .45), and addition of CP (positive β) to the rumen pH model increased R^2 to .55. Crude protein concentration was related to ruminal NH_3 level (positive β; R^2 = .42), and inclusion of ADFI (positive β) into the model improved the R^2 to .47.

(Key Words: Fluid Dilution Rate, Fermentation, Volatile Fatty Acids, pH, Crude Protein.)

Introduction

Disparity has arisen concerning the relationship of rumen fluid dilution rate (FDR) to rumen fermentation. Molar proportion of propionate (Pr) has varied inversely with FDR (Harrison et al., 1975; Hodgson and Thomas, 1975; Thomson et al., 1978; Crawford et al., 1980; Estell et al., 1982). A concomitant elevation of acetate (Ac) proportion often accompanies increases in FDR (Harrison et al., 1975, 1976; Thomson et al., 1978; Estell et al., 1982). Nevertheless, numerous reports show either no effect of FDR on molar proportions of volatile fatty acids (VFA) or the reverse relationship for Ac and(or) Pr (Abe and Kumeno, 1973; Isaacson et al., 1975; Czerkawski and Breckenridge, 1977; Kennedy and Milligan, 1978; Schaetzel and Johnson, 1981; Hoover et al., 1984). Response of other rumen fermentation characteristics [molar proportion of butyrate (Bu), total VFA concentration, pH and NH_3 concentration] to FDR alteration has been inconsistent, but data are limited.

Moreover, few data are available regarding effects of dietary constituents on FDR. Slower FDR has been associated with increased dietary concentrate level (Cole et al., 1976; Prins and

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Clarke, 1980; Huntington et al., 1981; Goetsch and Galyean, 1982) and decreased dry matter intake (Grovum and Williams, 1973; Kennedy and Milligan, 1978; Galyean et al., 1979; Evans, 1981; Adams and Kartchner, 1984). Both elevated roughage percentage and increased dry matter intake should increase FDR (Owens and Isaacson, 1977).

This study examined interrelationships of rumen fermentation measurements, FDR and fluid volume, body weight, dietary composition and intake with data from seven beef steer experiments.

Experimental Procedures

Data Compilation. Seven previous studies at New Mexico State University were compiled, and data were used to examine relationships among FDR, fermentation patterns and dietary constituents. Although these studies were conducted with specific, unrelated goals, each trial provided similar information. Data from studies by Adams et al. (1981; trial 1), Galyean and Chabot (1981; trial 2), Goetsch and Galyean (1982, 1983; trial 3 and 4, respectively), McCollum (1983; trial 5) and McCollum and Galyean (1983a,b; trial 6 and 7, respectively) were included in the compilation. A brief description of each trial appears in table 1.

Each study used Hereford or Hereford × Angus rumen-cannulated steers. Methodology for measurement of rumen FDR and rumen fluid volume was similar for all trials, in that a pulse-dose of an ethylenediaminetetraacetate-chelated metal was administered and a series of rumen samples was collected postdosing. Calculations were as described by McCollum and Galyean (1983a).

Data were screened and information common to all trials was recorded. Concentrations of crude protein (CP), acid detergent fiber (ADF) and ash (ASH) were available in all seven studies. Metabolizable energy concentration (ME; NRC, 1976) was computed for each diet. In addition, dry matter intake (DMI), crude protein intake (CPI), acid detergent fiber intake (ADFI), ash intake (ASHI) and metabolizable energy intake (MEI) were available for each steer. Metabolizable energy values for range forage (trial 5; table 1) were unavailable, thus, digestible organic matter obtained from in vitro organic matter digestibility determinations was converted to digestible energy (DE) concentration by the equation of Rittenhouse et al. (1971) and converted to ME by multiplication of DE by .82 (NRC, 1976).

Because the seven experiments were conducted with independent objectives, and frequent rumen sampling was required to measure FDR, a large number of rumen samples was generated and variation in sampling times occurred. However, most studies included determination of pH, molar proportions of Ac, Pr and Bu, total VFA concentration and NH_3 concentration at 3 or 4 h postfeeding. These values were considered to be close enough in time to represent adequately fermentation characteristics shortly after feeding. Exceptions were NH_3 concentration in trial 3 (analyzed only at 1 h postfeeding) and VFA concentration and molar proportions in trial 4 (only the mean of values for 0, 3, 6, 9 and 12 h postfeeding available). No time × treatment interaction existed in trial 4 for VFA proportions or concentration, so mean values should accurately depict 3-h values. Means and standard deviations of FDR, rumen fluid volume (FVOL), steer body weight, dietary variables and fermentation characteristics for each trial and for the seven trials combined are shown in table 2.

Statistical Analysis. The General Linear Models (GLM) procedure of Statistical Analysis System (SAS, 1979) was used to assess relationships between fermentation variables and FDR. For each trial and across the seven trials, Ac, Pr, Bu, VFA, pH and NH_3 (dependent variables) were individually regressed on FDR. Stepwise procedures of SAS with the maximum R^2 option (SAS, 1979) were used to describe rumen FDR and FVOL for the seven trials combined, with the nine dietary variables and body weight (WT) serving as independent variables. Stepwise procedures were used also to describe each of the six fermentation variables (across trials), with WT, FDR and the nine dietary variables as independent variables.

For all stepwise analyses, a maximum of eight variables was allowed to enter the equation. The best models containing one to eight significant variables are reported. Standard error of the estimate ($s_{y \cdot x}$) for each equation was the (mean square error)$^{-2}$ (Draper and Smith, 1966). Twenty-six steers were used in the seven studies. Each period was considered as an independent observation, resulting in 133 separate determinations of FDR, FVOL, WT and each fermentation and diet variable. The decision to consider repeated observations on the same animal as independent was supported

TABLE 1. DESCRIPTION OF SEVEN BEEF STEER TRIALS THAT PROVIDED DATA FOR PRESENT STUDY

Trial no.	n[a]	p[b]	Diet	Feeding schedule	Feeding level	Statistical design	Treatments[c]	EDTA[d]-chelated marker	Length of adaptation, d	No. of replications/period	Times postdosing of rumen sampling, h
1	5	5	Steam-flaked milo, alfalfa and molasses (50% concentrate)	Twice daily	Ad libitum	5 X 5 Latin square	Yeast culture, monensin, 2.5 and 5% sodium bicarbonate	Chromium	13	1	0, 4, 8, 12 and 24
2	5	5	Cottonseed hulls and 2.6 kg cottonseed meal-milo based supplement	Once daily	Ad libitum (hulls)	5 X 5 Latin square	McDougall's buffer salts, sodium bentonite, cement kiln dust and clinoptilolite	Chromium	13	1	0, 4, 8, 12, 16, 20 and 24
3	4	2	Steam-flaked milo and alfalfa hay	Twice daily	1.67 X NE_m[f]	Crossover	25 vs 75% concentrate	Cobalt	14	2	0, 1, 3, 6, 9, 12, 24 and 36
4	4	2	Corn-based 75% concentrate	Twice or eight times daily	1.67 X NE_m	Crossover	Twice vs eight feedings/day	Cobalt	16	1	0, 1, 3, 6, 9, 12, 24 and 36
5[e]	6	6	Blue grama rangeland	Free grazing	Ad libitum	Completely randomized	Stage of forage development	Cobalt	9	1	0, 4, 8, 12 and 24
6	4	4	Milo-based 85% concentrate	Twice daily	2 X NE_m	4 X 4 Latin square	0, 1.25, 2.5 and 5% clinoptilolite	Cobalt	9	2	0, 3, 6, 9, 12 and 24
7	8	2	Prairie hay	Once daily	Ad libitum (hay)	Crossover	Cottonseed meal supplementation (.8 kg)	Cobalt	22	1	0, 3, 4, 6, 9, 12, 15 and 24

[a]The same four steers were used in trials 3 and 6, and all six steers used in trial 5 were also used in trial 7. Total steers used in all trials = 26.

[b]p = no. of periods.

[c]Treatments used to evaluate changes in rumen fluid dilution rate.

[d]EDTA = ethylediaminetetraacetic acid.

[e]One observation was missing in the first period of trial 5.

[f]NE_m = net energy for maintenance.

TABLE 2. RUMINAL AND DIETARY CHARACTERISTICS FOR THE SEVEN BEEF STEER TRIALS[a]

Item	Trial 1		Trial 2		Trial 3		Trial 4		Trial 5		Trial 6		Trial 7		Combined	
	$\bar{x}$	SD[a]	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Fluid dilution rate, %/h	10.5	1.8	9.1	2.3	5.3	1.2	4.6	.6	11.1	2.7	6.8	1.1	9.6	3.1	9.2	3.0
Fluid volume, liters	40.6	10.1	48.2	21.7	70.3	13.7	118.7	18.1	35.1	8.0	47.4	15.9	25.6	6.8	46.1	25.0
Acetate, mol/100 mol	61.2	4.1	72.9	4.6	64.4	3.0	61.3	1.4	69.3	3.4	55.2	4.0	70.4	2.6	66.1	6.9
Propionate, mol/100 mol	25.9	3.8	19.0	3.6	19.4	1.7	21.9	1.9	17.3	1.4	35.3	3.0	17.5	1.5	21.8	6.5
Butyrate, mol/100 mol	10.0	2.7	7.0	1.6	11.1	.7	10.5	1.6	9.6	1.5	7.1	1.8	9.5	.9	9.0	2.2
VFA, mM[b]	90.3	22.7	127.9	44.9	81.6	8.3	98.1	9.2	92.2	12.8	106.5	11.4	89.4	11.7	99.6	27.6
Ammonia, mg/100 ml	29.8	11.6	10.4	6.8	20.1	10.5	39.2	19.4	11.9	8.7	3.8	1.3	4.5	3.0	15.2	13.9
pH	6.3	.4	6.5	.2	6.0	.3	6.1	.3	6.4	.3	5.5	.3	6.5	.3	6.3	.4
Body weight, kg	423.0	37.3	346.9	25.2	472.0	19.8	316.9	10.0	299.2	44.7	411.7	23.5	222.1	17.2	347.1	78.1
DMI, kg/d[c]	10.5	1.9	9.5	.9	8.4	1.0	5.7	.1	6.5	1.8	6.6	.3	4.5	1.4	7.7	2.4
ME, Mcal/kg[de]	2.4	.03	1.8	.1	2.5	.2	2.9	0	1.6	.3	2.7	.1	1.9	.1	2.1	.5
MEI, Mcal/d[ef]	25.7	4.5	17.1	1.5	20.9	1.0	16.6	.4	10.4	4.0	18.0	.8	8.6	2.8	16.2	6.6
CP, %[eg]	15.9	.3	7.1	.4	18.0	1.7	17.9	0	10.5	3.4	12.1	.2	8.5	2.6	11.7	4.2
CPI, kg/d[eh]	1.7	.3	.7	.06	1.5	.3	1.0	.03	.7	.3	.8	.04	.4	.2	.9	.5
ADF, %[ei]	24.4	2.2	49.4	2.7	19.0	5.8	16.0	0	42.1	4.8	14.1	1.2	42.1	1.8	33.8	13.4
ADFI, kg/d[ej]	2.6	.5	4.7	.6	1.6	.7	.9	.02	2.7	.7	.9	.1	1.9	.6	2.6	1.3
ASH, %[ek]	9.7	1.0	13.7	1.4	9.7	2.3	9.6	0	16.5	2.3	8.3	1.9	9.8	.2	12.1	3.5
ASHI, kg/d[el]	1.0	.2	1.3	.2	.8	.3	.5	.01	1.1	.4	.6	.1	.4	.1	.9	.4

[a]SD = standard deviation.

[b]VFA = total volatile fatty acids.

[c]DMI = dry matter intake.

[d]ME = metabolizable energy concentration.

[e]Dry matter basis.

[f]MEI = metabolizable energy intake.

[g]CP = crude protein concentration.

[h]CPI = crude protein intake.

[i]ADF = acid detergent fiber concentration.

[j]ADFI = acid detergent fiber intake.

[k]ASH = ash concentration.

[l]ASHI = ash intake.

by a lack of consistent animal effect on fermentation characteristics vs FDR based on preliminary plot analyses. Furthermore, GLM procedures were conducted on these variables by steer and compared with models with all steers included. Root mean square error, $(MSE)^{-2}$, of overall models were of the same magnitude as $(MSE)^{-2}$ of individual steer models, and individual $(MSE)^{-2}$ were usually similar to overall $(MSE)^{-2}$ for a given model. Based on these computations, steer effects were ignored and FDR estimates from a given steer during different periods were considered independent observations.

Results and Discussion

Fermentation and Fluid Dilution Rate. Relationship of FDR with each fermentation variable was examined by trial and across trials (table 3). Fluid dilution rate and Ac were positively related ($P<.10$) in trials 1 and 3, but negatively related in trials 2 ($P<.01$), 5 ($P<.001$) and 7 ($P<.05$). Elevated FDR was associated with increased Pr in trials 2 ($P<.001$), 5 ($P<.001$) and 7 ($P<.05$). A positive relationship between FDR and Bu was observed in trials 5 ($P<.001$) and 7 ($P<.05$), but a negative relationship existed in trial 3 ($P<.01$). Total VFA concentration was positively related to FDR in trial 5 ($P<.01$). Ammonia concentration and FDR were positively related in trial 5 ($P<.01$) but negatively related in trial 1 ($P<.10$). In trials 1 and 3, pH and FDR were positively related ($P<.10$), but were negatively related ($P<.01$) in trial 5. Although regression coefficients were often nonsignificant for FDR vs fermentation measurements, their magnitude and varying directions reveal a variable response of fermentation characteristics to altered FDR. Examination of the combined analysis of all seven trials (table 3) further substantiates this variability. Only two relationships were significant in the combined analysis; negative ($P<.05$) and positive ($P<.001$) relationships were noted between FDR and Pr and pH, respectively.

Although a negative and positive relationship of Pr and Ac, respectively, with FDR has been reported previously, it is often not the case (table 3). The present data and other reports (Isaacson et al., 1975; Kennedy and Milligan, 1978; Hoover et al., 1984) do not show consistent positive changes in Ac and negative changes in Pr with increased FDR.

Diet effects may have caused differences in Ac and Pr shifts upon FDR alteration. Increased molar proportion of propionate has been associated with elevated proportion of dietary concentrates (Reid et al., 1957; Rumsey et al., 1970) and reduced FDR (Cole et al., 1976; Huntington et al., 1981). Trials in which high concentrate diets were fed generally showed slower FDR, higher Pr and lower Ac proportion (table 2), which may have been responsible for depressed ($P<.05$) Pr and a trend for elevated ($P>.10$) Ac with increased FDR in the combined analysis. However, Harrison et al. (1975) observed an inverse relationship of Pr with FDR when FDR was altered without a dietary change. Also, Rogers et al. (1979) noted depressed Pr and elevated Ac when FDR was accelerated in cattle consuming a concentrate diet, but not with cattle fed a high roughage diet. Higher baseline FDR was observed for cattle fed the high roughage diet, indicating a low FDR in control animals may be necessary for a fermentation response to FDR manipulation. Hoover et al. (1984) also noted decreased Pr when FDR was increased from 4 to 8%/h and 8 to 12%/h, but no further effect occurred when FDR was increased to 16%/h. Sutton (1980) reported the effect of altering dietary concentrate level on FDR depends on initial and final proportion of dietary concentrate.

Response of Bu to FDR alteration was erratic for the seven individual trials (table 3) and was not related ($P>.10$) to FDR for the combined analysis. Lack of consistency among trials was also evident with respect to the effect of FDR on total VFA concentration (table 3). Only trial 5 exhibited a relationship ($P<.01$; positive β) of VFA concentration and FDR. In this pasture study, faster FDR was observed during stages of lush, more fermentable forage growth. Fluid dilution rate and VFA concentration were not related ($P>.10$) when data were combined across trials (table 3).

Kennedy and Milligan (1978) noted lower ruminal NH_3 concentration in sheep with faster FDR. In the present study, however, only trial 1 exhibited a negative relationship ($P<.10$) between NH_3 concentration and FDR, although a trend ($P>.10$) for negative relationships was observed in trials 2, 6 and 7 (table 3). In trial 5, a positive relationship ($P<.01$) existed between these variables, perhaps due to a higher soluble N concentration in more lush forages.

Elevated FDR could hasten removal of

ASH = ash intake.

TABLE 3. RELATIONSHIP OF FLUID DILUTION RATE AND FERMENTATION CHARACTERISTICS FOR SEVEN BEEF STEER TRIALS

Trial no.	Statistic	Acetate, mol/100 mol	Propionate, mol/100 mol	Butyrate, mol/100 mol	VFA[a], mmol/liter	Ammonia, mg/100 ml	pH
1	n	25	25	25	25	25	25
	β	.82†	−.54 NS[b]	−.47 NS	−1.41 NS	−2.50†	.07†
	$s_{y\cdot x}$	3.88	3.79	2.58	23.03	10.96	.35
	R^2	.133	.066	.101	.013	.151	.119
2	n	25	25	25	25	25	25
	β	−1.07**	1.03***	.11 NS	−.73 NS	−.60 NS	−.01 NS
	$s_{y\cdot x}$	3.94	2.71	1.62	45.80	6.82	.22
	R^2	.287	.443	.026	.001	.041	.026
3	n	8	8	8	8	8	8
	β	1.73†	−.72 NS	−.47**	.83 NS	.88 NS	.14†
	$s_{y\cdot x}$	2.28	1.62	.37	8.87	11.28	.21
	R^2	.491	.247	.733	.014	.010	.425
4	n	8	8	8	8	8	8
	β	−.69 NS	1.92 NS	−1.10 NS	7.13 NS	19.92 NS	−.32 NS
	$s_{y\cdot x}$	1.45	1.63	1.55	8.80	16.62	.29
	R^2	.086	.361	.172	.212	.370	.331
5	n	35	35	35	35	35	35
	β	−.98***	.28***	.35***	2.31**	1.82***	−.04**
	$s_{y\cdot x}$	2.22	1.16	1.17	11.31	7.28	.23
	R^2	.598	.309	.403	.243	.325	.206
6	n	16	16	16	16	16	16
	β	−.98 NS	.49 NS	.39 NS	.49 NS	−.04 NS	.02 NS
	$s_{y\cdot x}$	3.95	3.00	1.81	11.77	1.37	.29
	R^2	.073	.033	.056	.002	.001	.008
7	n	16	16	16	16	16	16
	β	−.47*	.27*	.15*	1.11 NS	−.22 NS	.03 NS
	$s_{y\cdot x}$	2.18	1.24	.78	11.60	3.01	.25
	R^2	.324	.335	.267	.087	.051	.145
Combined	n	133	133	133	133	133	133
	β	.28 NS	−.37*	.10 NS	.01 NS	−.16 NS	.05***
	$s_{y\cdot x}$	6.86	6.40	2.19	27.70	13.94	.40
	R^2	.015	.029	.017	.000	.001	.116

[a]VFA = total volatile fatty acid concentration.

[b]NS = nonsignificant (P>.10).

†P<.10.

*P<.05.

**P<.01.

***P<.001.

acidic end-products and increase pH. Trials 1 and 3 ($P<.10$) and the combined analysis ($P<.001$) demonstrated a positive relationship for pH and FDR. A negative relationship for these two variables was noted in trial 5, probably because of greater fermentability of more lush forage. Based on information from these seven trials, effects of FDR alteration on fermentation may be somewhat predictable for a given set of conditions. Effects of FDR are less definite, however, across a wide set of conditions.

Fluid Dilution Rate and Diet. Dietary characteristics and body weight (table 2) from the seven studies were used as independent variables to describe FDR (table 4) with stepwise regression. The same approach was also used to describe FVOL (table 4).

Rumen FDR was best described by ASHI, with FDR increasing slightly per unit increase in ASHI; however, R^2 was only .16. The fact that ASHI was the most important determinant of FDR agrees with reports of elevated FDR with increased consumption of mineral salts (Harrison et al., 1975, 1976; Rogers et al., 1979). Increased quantities of osmotically active material in the rumen from infusion of hypertonic solutions seemingly causes increased water influx and may increase water intake, which should increase liquid outflow (Rogers et al., 1979). The best two-variable model (R^2 = .36) indicated a negative relationship of WT and a positive association of DMI with FDR. Increased DMI has increased FDR in previous studies (Grovum and Williams, 1973; Kennedy and Milligan, 1978; Galyean et al., 1979; Adams and Kartchner, 1984). Evans (1981) assessed factors affecting FDR and concluded that DMI was the most important factor controlling FDR for both cattle and sheep, which could be due to the fact that DMI often parallels water intake. Harrison et al. (1975) detected no effect of H_2O infusion on FDR; however, water intake was not measured in control vs infused animals. The inverse relationship between body size and FDR was similar to results of Poppi et al. (1981), who noted faster FDR in smaller animals. The best three-variable model contained DMI, WT and ASH (R^2 = .38). The best six-variable model for FDR explained 50% of the variation in FDR and contained MEI and ADFI, as well as the four previously mentioned variables. Partial regression coefficients for both MEI and ADFI were negative. Decreased MEI should increase FDR because it reflects elevated roughage intake, which should stimulate salivation and increase rumen fill (Owens and Isaacson, 1977). The negative effect of ADFI on FDR is surprising because coarser feeds stimulate salivation (Putnam et al., 1966). However, the magnitude of the coefficient was extremely small, and MEI had

TABLE 4. EQUATIONS DESCRIBING RUMEN FLUID DILUTION RATE AND FLUID VOLUME[a]

Equation[bc]	R^2	$s_{y \cdot x}$
FDR = 6.19 + .003 (ASHI)	.1669	2.75
FDR = 12.11 + .001 (DMI) −.03 (WT)	.3623	2.42
FDR = 9.69 + .001 (DMI) −.02 (WT) + .14 (ASH)	.3852	2.38
FDR = 1.24 + .002 (DMI) −.03 (WT) + .96 (ASH) −.01 (ASHI)	.4408	2.28
FDR = 4.94 + .004 (DMI) −.04 (WT) + .68 (ASH) −.009 (ASHI) −.57 (MEI) −.002 (ADFI)	.5022	2.17
FVOL = −1.14 + 22.62 (ME)	.2035	22.42
FVOL = −44.91 + 32.47 (ME) + 1.92 (ASH)	.2382	22.01
FVOL = −70.04 + .009 (DMI) + 9.15 (CP) −.09 (CPI) + .08(WT)	.3474	20.53
FVOL = −3.35 −4.76 (ASH) + 7.99 (CP) −.08 (CPI) + .08(WT) + .06 (ASHI)	.3586	20.44

[a]Only models in which all selected variables were significant ($P<.05$) are presented.

[b]n = 133.

[c]FDR = fluid dilution rate, %/h; ASHI = ash intake, kg/d; DMI = dry matter intake, kg/d; WT = body weight, kg; ASH = ash concentration, %; MEI = metabolizable energy intake, Mcal/d; ADFI = acid detergent fiber intake, kg/d; FVOL = fluid volume, liters; ME = metabolizable energy concentration, Mcal/kg; CP = crude protein concentration, %; CPI = crude protein intake, kg/d.

been accounted for. In addition, in many of the seven trials, roughage was fed in the ground form and buffers were fed, which may have confounded relationships.

When FVOL was described by the same set of variables as with FDR (table 4), ME was the best predictor of FVOL (R^2 = .20). As diet ME rose, FVOL also increased. In contrast, Putnam et al. (1966) observed decreased rumen volume as dietary concentrate proportion increased. Galyean et al. (1979) observed lower FVOL with increasing intake of a high concentrate diet, and suggested that increased rumen dry matter may have forced more liquid from the rumen. Huntington et al. (1981) reported that elevated concentrate proportion may have increased DMI and increased FVOL. Possibly, diets with increased concentrate proportions may occupy less space because of a more rapid degradation and, consequently, may force less fluid outflow, which could explain higher fluid volumes associated with diets of greater ME. The best two-variable model for FVOL also contained ASH (positive β; R^2 = .23). Elevated ASH should increase the amount of osmotically active material in the rumen, which could cause water influx and consequently increase FVOL. In the four-variable model, a slight positive relationship of DMI and FVOL was observed. Purser and Moir (1966) and Putnam et al. (1966) showed that rumen volume (fluid + particulate) increased when DMI increased. Adams and Kartchner (1984) reported an inverse relationship between DMI and FVOL. The four-variable model for FVOL also contained WT and CP (positive β) and CPI (negative β). A positive relationship between WT and FVOL would be expected, because Purser and Moir (1966) observed a positive correlation between sheep weight and empty rumen weight. Also, CPI tended to be higher with rapidly fermented diets (table 2) that would be degraded more quickly and allow for more fluid space. Generally, FVOL was not effectively described by the variables offered for selection, because R^2 was small and $s_{y \cdot x}$ was large for equations describing FVOL.

Fermentation and Diet. Because FDR did not appear to be a major director of fermentation, stepwise regression was employed to describe each of the six fermentation variables (table 5) with WT, FDR and the nine dietary components (table 2) as independent variables. Using this procedure, the best one-variable model for Ac contained ADF (positive β, R^2 = .71). Enhancement of molar proportion of Ac by dietary fiber in ruminants is well documented (Reid et al., 1957; Rumsey et al., 1970). A 4% increase in R^2 was achieved when FDR and CP entered, with most of this increase attributed to FDR; however, in contrast to many literature reports, FDR was negatively related to Ac.

Molar proportion of propionate was best described by, and negatively related to, ADF (R^2 = .51; table 5), which agrees with reports that Pr and diet roughage proportion are inversely related (Reid et al., 1957; Rumsey et al., 1970). The second variable selected was CP, which exerted a negative effect on Pr and increased R^2 by 11%. The effect of CP on Pr may have been an artifact created by the possibility that feeds high in ADF were also high in CP. A positive effect of MEI on Pr was noted in the three-variable model, which accounted for an additional 7% of the variation in Pr. An additional 2% of the variation in Pr was explained by FDR. In contrast to previous reports, the partial coefficient for FDR was positive when effects of dietary energy, fiber and protein were accounted for. A five-variable model (R^2 = .73) contained WT, which had a small, positive β.

The variable best related to Bu proportion was CP (R^2 = .23; table 5), which is in agreement with Church (1975). The two-variable model for Bu contained ME (negative β; R^2 = .31). Reid et al. (1957) observed that addition of corn to alfalfa diets decreased ruminal Bu proportion, but Rumsey et al. (1970) found elevated Bu with increased concentrate level. The third variable that entered the Bu model was WT, but the partial coefficient was small (−.006).

Total VFA concentration was best described by ADFI (R^2 = .14; table 5), with a small (.008), positive β. The best two-variable model for VFA contained ME (R^2 = .18). The positive partial β was large (13.49), suggesting dietary energy density is related to degree of fermentation. Other researchers have shown increased rumen VFA concentration with elevated dietary concentrate (Putnam et al., 1966; Esdale et al., 1968). The three-variable model contained CPI (R^2 = .29). Addition of other variables resulted in small increases in R^2.

Generally, variables representing intake were more often selected to describe VFA concentration, while molar proportions were best described by dietary concentration variables.

This finding was expected, because total substrate available should reflect fermentation capacity, while individual dietary components should dictate microbial populations and pathways and, consequently, end-products.

Models describing molar proportions of Ac and Pr had higher R^2 values than Bu and VFA concentration, suggesting Ac and Pr are better indicators of change of fermentation status, while Bu and total VFA are explained by random variation or factors yet to be identified. Total VFA description might have been more effective if total production rather than concentration at 4 h postfeeding had been available, because absorption and microbial metabolic state may complicate interpretation of concentration values. Diet may also affect VFA concentration at 4 h postfeeding, because the VFA peak is later with forage diets than with high concentrate diets (Phillipson, 1942).

The best variable for describing pH was ADF (R^2 = .45; table 5). Elevated pH in conjunction with elevated fiber intake was expected because high grain diets depress rumen pH (Putnam et al., 1966; Rumsey et al., 1970) due to more rapid fermentation, causing greater acidic

TABLE 5. EQUATIONS DESCRIBING FERMENTATION VARIABLES[a]

Equation[bc]	R^2	$s_{y \cdot x}$
Ac = 51.44 + . 43 (ADF)	.7145	3.69
Ac = 54.31 + .47 (ADF) −.44 (FDR)	.7467	3.49
Ac = 50.01 + .53 (ADF) −.50 (FDR) + .24 (CP)	.7542	3.45
Pr = 33.47 −.34 (ADF)	.5085	4.55
Pr = 50.14 −.55 (ADF) −.84 (CP)	.6233	4.00
Pr = 46.84 −.52 (ADF) −1.09 (CP) + .33 (MEI)	.6952	3.61
Pr = 53.25 −.78 (ADF) −1.13 (CP) + .39 (FDR) + .002 (ADFI)	.7189	3.48
Pr = 28.37 −.44 (ADF) −1.10 (CP) + .55 (FDR) + 4.37 (ME) + .02 (WT)	.7258	3.45
Bu = 6.05 + .25 (CP)	.2325	1.94
Bu = 8.02 + .42 (CP) −1.86 (ME)	.3150	1.84
Bu = 9.05 + .44 (CP) −1.44 (ME) −.006 (WT)	.3472	1.80
VFA = 79.54 + .008 (ADFI)	.1405	25.68
VFA = 44.63 + .01 (ADFI) + 13.49 (ME)	.1842	25.12
VFA = 19.51 + .01 (ADFI) + 32.03 (ME) −.02 (CPI)	.2910	23.51
VFA = 38.53 + .04 (ASHI) + 17.97 (ME) −.06 (CPI) + 2.62 (MEI)	.3248	23.03
VFA = 180.76 + .03 (ADFI) + .05 (ASHI) −3.64 (CP) + 8.11 (MEI) −1.70 (ADF) −.03 (DMI)	.3462	22.84
pH = 5.54 + .02 (ADF)	.4551	.32
pH = 4.52 + .03 (ADF) + .05 (CP)	.5525	.29
pH = 4.56 + .06 (ADF) + .05 (CP) −.0004 (ADFI) −.10 (ASH) + .001 (ASHI)	.6006	.28
pH = .94 + .13 (ADF) + .21 (CP) −.001 (ADFI) −.14 (ASH) + .002 (ASHI) −.002 (CPI) + .0005 (DMI)	.6326	.27
NH_3 = −10.26 + 2.17 (CP)	.4266	10.57
NH_3 = −20.76 + 2.52 (CP) + .002 (ADFI)	.4713	10.18
NH_3 = −21.14 + 2.72 (CP) + .39 (ADF) + .82 (MEI) −.72 (FDR) −.04 (WT)	.5101	9.92

[a]Only models in which all selected variables were significant ($P<.05$) are presented.

[b]$n = 133$.

[c]Ac = acetate, mol/100 mol; ADF = acid detergent fiber concentration, %; FDR = fluid dilution rate, %/h; CP = crude protein concentration, %; Pr = propionate, mol/100 mol; MEI = metabolizable energy intake, Mcal/d; ADFI = acid detergent fiber intake, kg/d; ME = metabolizable energy concentration, Mcal/kg; WT = body weight, kg; Bu = butyrate, mol/100 mol; VFA = volatile fatty acids, mM; CPI = crude protein intake, kg/d; ASHI = ash intake, kg/d; DMI = dry matter intake, kg/d; ASH = ash concentration, %; pH = rumen pH; NH_3 = rumen ammonia, mg/100 ml.

end-product production (Briggs et al., 1957; Reid et al., 1957; Rumsey et al., 1970). Roughage diets stimulate saliva production (Owens and Isaacson, 1977), which should increase rumen pH. In addition, many of the diets in the present study contained alfalfa, which has a natural buffering capacity (Church, 1975). The second variable to enter the model was CP, which was positively related to pH and explained an additional 10% of the variation. Increased intake of CP should increase NH_3 accumulation (Robertson and Hawke, 1965), and Adams and Kartchner (1984) reported a positive relationship between NH_3 and pH. Other variables which entered in later models included three variables with negative β (ASH, ADFI and CPI) and two with positive β (ASHI and DMI). The positive relationship of pH and DMI was surprising, because Rumsey et al. (1970) observed depressed pH with elevated DMI. The magnitude of partial coefficients of later entries was small and accounted for a relatively small proportion of the variation in pH.

The variable most closely related (positive β, R^2 = .43) to NH_3 concentration was CP (table 5). Increased protein intake increased rumen NH_3 concentration in other studies (Briggs et al., 1957; Robertson and Hawke, 1965) due to microbial deamination of nitrogenous components (Hungate, 1966). An additional 5% of the variation in NH_3 was explained by ADFI (positive β), perhaps due to the N content of alfalfa, a common fiber component in many of our diets. In further models, MEI and ADF (positive β) and WT and FDR (negative β) entered with small increases in R^2.

In summary, fermentation responses to altered FDR were complex and complicated by diet and microbial interactions. Relationships between FDR and fermentation often regarded as absolute should be questioned. Such relationships possibly exist, however, within specific conditions. Other factors must be identified in order to manipulate FDR for more efficient animal production.

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